JACQUEMONTIA OVALIFOLIA (CONVOLVULACEAE) IN AFRICA, NORTH AMERICA, AND THE HAWAIIAN ISLANDS¹

KENNETH R. ROBERTSON²

ABSTRACT

Jacquemontia ovalifolia (Choisy) Hallier f. is one of the most broadly distributed species of the genus. A study of herbarium material from throughout its range lead to the recognition of three subspecies: subsp. ovalifolia from Africa, subsp. obcordata (Millspaugh) Robertson from Mexico and the West Indies, and subsp. sandwicensis (A. Gray) Robertson from the Hawaiian Islands. The species is probably of American origins and was dispersed at an unknown time by unknown means to Africa and Hawaii. The nomenclatural histories of the species and subspecies are reviewed, and a complete taxonomic treatment is presented.

While preparing a revision of the New World species of *Jacquemontia* Choisy, taxonomic and nomenclatural difficulties were encountered with what has been called *J. subsalina* Britton or *J. obcordata* (Millspaugh) House, and it became clear that the problems could be resolved only by studying this taxon and its relatives on a world-wide basis, namely Africa, Mexico and the West Indies, and the Hawaiian Islands.

NOMENCLATURAL HISTORY

AFRICAN POPULATIONS

Vahl (1798) described a plant collected by von Rohr supposedly in "India Occidentali" as *Convolvulus ovalifolius*; the type and an isotype are conserved in Copenhagen (Fig. 3). This specimen is discordant with any known American plant. Monachino (1958) realized this from an examination of the type and concluded that it was instead from the Hawaiian Islands. Verdcourt (1963) considered the von Rohr collection identical with plants from Africa, although he stated that the type specimen probably was from Trinidad. In comparing the von Rohr collection with material from the West Indies, Mexico, the Hawaiian Islands, and Africa, I concur with Verdcourt that the type of *Convolvulus ovalifolius* Vahl belongs to the same taxon as the African plants. Julius von Rohr collected primarily in the West Indies and northwestern South America during the late Eighteenth Century; however, Junghans (1961) notes that von Rohr did collect a few plants in Danish Guinea [now Ghana] and that there are

¹Extracted, rewritten, and augmented from a dissertation submitted to the Department of Biology and the Faculty of the Graduate School of Washington University, St. Louis, in partial fulfillment of the requirements for the degree Doctor of Philosophy. The scanning electron photomicrographs of pollen were taken by Dr. Umesh Banerjee of the Arnold Arboretum on an Advanced Metals Research High Resolution Scanning Electron Microscope Model 900 located at Harvard University. Microfisches are cited by the method of Hepper (1968). All specimens cited have been examined, unless otherwise indicated.

² Washington University and the Missouri Botanical Garden, St. Louis. *Present address:* Arnold Arboretum of Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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seven such specimens extant at Copenhagen. It seems very likely that the von Rohr collection of C. ovalifolius is from Danish Guinea.

Unfortunately, West (1793) had previously used Convolvulus ovalifolius for another plant (referred by Vahl to C. quinquepartitus Vahl = Jacquemontia havanensis (Jacquin) Urban), attributing the description to Vahl (see also Urban, 1898, and Monachino, 1958); thus, C. ovalifolius Vahl is illegitimate. Choisy (1834) transferred this species to Ipomoea; nomenclaturally, I. ovalifolia Choisy must be regarded as a new name with the same type as C. ovalifolius Vahl. Convolvulus coeruleus Schumacher, published in 1827, is earlier than I. ovalifolia Choisy but is itself a later homonym of C. coeruleus Sprengel (1824), which is a taxonomic synonym of J. pentantha (Jacquin) G. Don. Later, Welwitsch (1858) described Ipomoea oleracea based on plants collected by himself in Angola. This name is clearly a synonym of Jacquemontia ovalifolia.

AMERICAN POPULATIONS

Based on Vahl's incorrect allocation of the von Rhor collection to the West Indies, later authors such as Choisy (1834, 1845) listed the species as occurring there. Actually, related plants are found on certain islands in the Caribbean and in eastern Mexico and were gathered early by Pavón, Sessé and Mociño, and Wullschlägel. These collections mostly were referred to *Jacquemontia* (*Convolvulus, Ipomoea*) *ovalifolia*. The American plants do differ from the African ones and can be recognized as a distinct taxon. Millspaugh (1900) described a new species, *Convolvulus obcordatus*, from material he collected in Yucatán, Mexico (Fig. 5). This name was transferred to *Jacquemontia* by House (1921), who considered the Mexican plants distinct enough from the West Indian plants to represent a separate species. Evidently unaware of Millspaugh's name, Britton (1925) delimited *J. subsalina* from Puerto Rico.

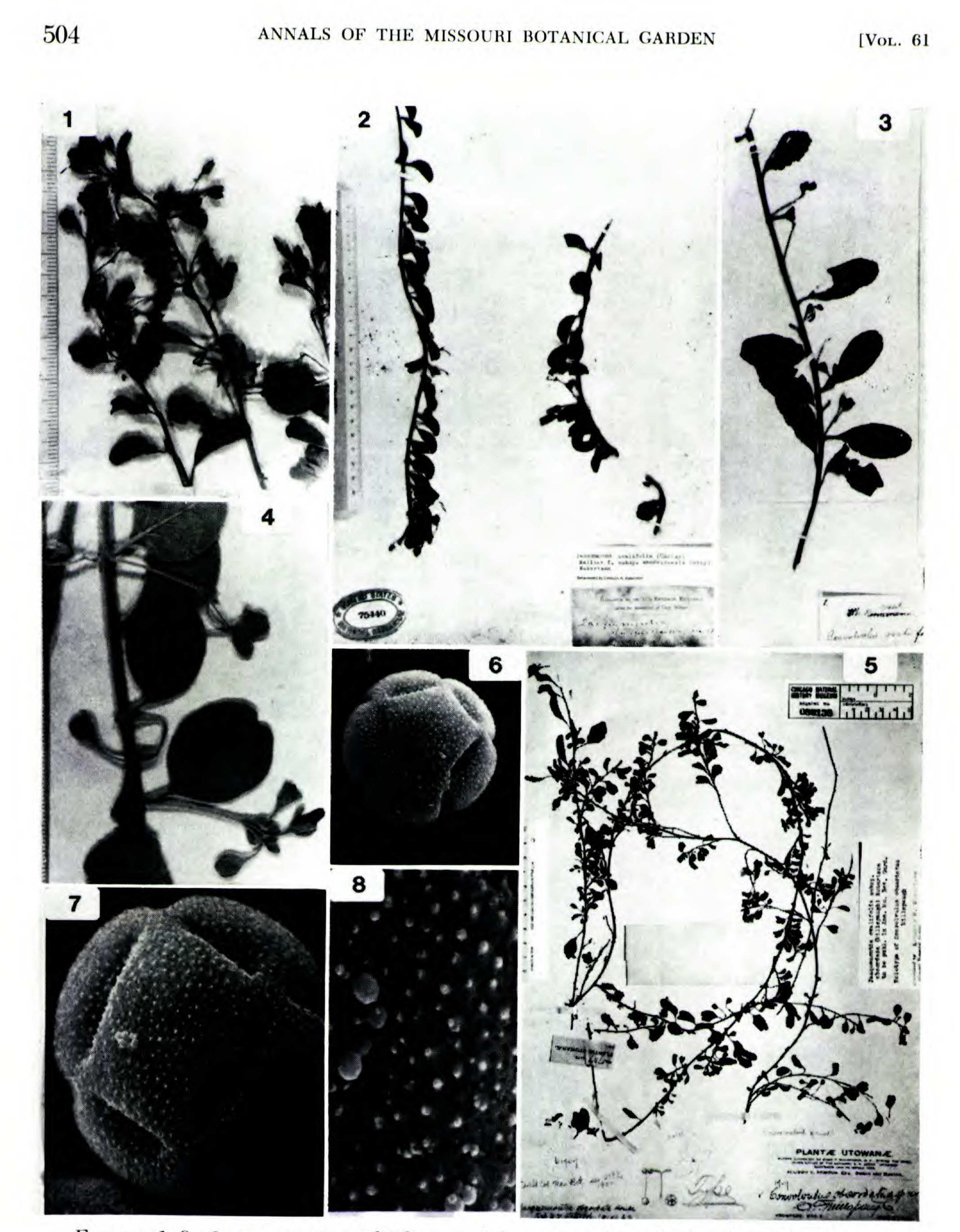
HAWAIIAN POPULATIONS

Early explorers to the Hawaiian Islands (named the Sandwich Islands by their discoverer Captain James Cook) such as Menzies and the Beechey and Wilkes Expeditions encountered similar plants, and Hooker and Arnott (1832), Choisy, and others referred these to Jacquemontia (Convolvulus, Ipomoea) ovalifolia. Asa Gray (1862), working with material from the U. S. Exploring Expedition, described J. sandwicensis for the Hawaiian plants (Fig. 2). Since then, this specific name generally has been applied to them. The African and American populations were even included under J. sandwicensis by Hallier

(1918).

RELATIONSHIPS AND DISCUSSION

The plants considered here have been placed in four genera: *Convolvulus* L., *Ipomoea* L., *Jacquemontia* Choisy, and *Montejacquia* Roberty. Such a diverse treatment is not uncommon in the Convolvulaceae where generic limits are notoriously ill-defined. The following attributes indicate that these plants are properly included within *Jacquemontia*: 2-armed trichomes; smooth pollen



FIGURES 1-8. Jacquemontia ovalifolia.—1. Subsp. obcordata, detail of branch with mature capsules (Moore 2129).—2. Type of J. sandwicensis A. Gray.—3. Type of Ipomoea ovalifolia

Choisy.—4. Portion of a densely pubescent plant of subsp. sandwicensis (Webster et al. 13986).—5. Type of Convolvulus obcordatus Millspaugh.—6–8. Scanning electron photomicrographs of acetolyzed pollen grains of subsp. obcordata (Moore 2129).—6. Polar view, \times 500.—7. Equatorial view, \times 1000.—8. Detail of pollen, a colpus to the left, 4 Ubisch bodies attached to the margin of the colpus, note the numerous punctae and spinules, \times 2500.

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with 15 colpi, 5 at each pole, 5 equatorial (Figs. 6-8); 2-locular and 4-ovulate ovaries; bilobed stigmas, the lobes flattened and shortly ellipsoidal or clavate; capsular fruit (Fig. 1); glabrous seeds with minute wings on the outer margins; and a base chromosome number of 9 (one count by Jones, 1968).

The current practice in regional floras is to treat plants from the different geographical areas as distinct species (Verdcourt, 1963; Adams, 1972; Degener & Degener, 1956). From a careful study of herbarium material from all three regions, and from comparisons to other species of the genus, I conclude that only one species should be recognized, Jacquemontia ovalifolia (Choisy) Hallier f., with three subspecies, subsp. ovalifolia in Africa, subsp. obcordata in the West Indies and Mexico, and subsp. sandwicensis in Hawaii. This species has the broadest distribution of any species of the genus. Within the genus, Jacquemontia ovalifolia may be distinguished by its ability to root at the nodes; blue to white, subrotate to shallowly campanulate corollas; elliptic to circular leaves with indented apices and noncordate bases; 2-armed and T-shaped trichomes; usually 2-4-valvate capsules; and minutely areolate and narrowly winged seeds. The only clearly related species is J. serpyllifolia (H.B.K.) Urban, an endemic of the serpentine hills and palm barrens in the western part of Cuba. These two species constitute a distinct section of the genus (to be described in a later paper).

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The geographical distribution of this species is perplexing, and it can probably never be known if the species was dispersed from one region of the world to another by natural means or by man. The total range does not seem to follow old exploration, merchant, slave trade, or missionary routes. Until it can be shown otherwise, it is presumed that the species is indigenous to the three areas. The genus is mostly American with the greatest diversity of forms in the West Indies, although the majority of species occur on the American mainland. No species is restricted to Africa. The African representatives of the genus are Jacquemontia ovalifolia, J. tamnifolia (L.) Grisebach, which also is found in the New World from Virginia to Dominica, Paraguay, Argentina, and Brazil, and J. paniculata (Burmann f.) Hallier f., which ranges from Africa and Madagascar to southeastern Asia, tropical Australia, and New Caledonia. Jacquemontia ovalifolia is the only species of the genus in Hawaii. Although widespread in its distribution in Caribbean America and Africa, this species is never very abundant there, while in Hawaii it is both ubiquitous and common. The comparative lack of competition in the isolated oceanic situation of the Hawaiian Islands may account for its plentifulness. It can be speculated that the species is of American origins, perhaps in the West Indies where its only related species, J. serpyllifolia, occurs, and it was dispersed at an unknown time by unknown means to Africa and Hawaii. The broad distribution of this species within each geographic area in which it occurs suggests that it must have a fairly efficient means of short-range dispersal. The seeds have a hard coat, as do many Convolvulaceae, and would probably pass intact through a bird's digestive system. Also, the seeds are small enough to be carried in mud on birds' feet. Morphologically, the seeds

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of the different subspecies of Jacquemontia ovalifolia do not differ significantly from one another or indeed from the other species of the genus, which are certainly not dispersed primarily by water. However, water is the agent used in theories presented to account for the long-range dispersal of this species to the Hawaiian Islands. The seeds of subsp. sandwicensis reportedly sink in sea water, and Guppy (1906) suggested that the original colonizing seeds might have rafted to Hawaii from North America in crevices of a drifting log. Ridley (1930) speculated that perhaps the ancestor of the Hawaiian Jacquemontia had buoyant seeds, and Carlquist (1967) adds that this plant is probably in a stage of transition with respect to loss of dispersibility. It seems to me that there is very little case for long-range dispersal of J. ovalifolia by water; birds could be the vector for both short- and long-range dispersal. The morphological distinctiveness of the plants from the three geographical areas indicates that reintroductions from one area to another do not occur frequently, if ever.

TAXONOMIC TREATMENT

Jacquemontia ovalifolia (Choisy) Hallier f., Bot. Jahrb. Syst. 16: 543. 1892.

Ipomoea ovalifolia Choisy, Mém. Soc. Phys. Genève 6: 449. 1834; Convolvulac. Orient., 67. Based on Convolvulus ovalifolius Vahl, non Vahl ex West.
? J. ovata Owerin ex Regel, Gartenflora 9: 271. pl. 300. 1860. Plants grown from seeds collected in Chili, no specimens known; illustration taken as the type.
Montejacquia bifida (Velloso) Roberty, Candollea 14: 33. 1952, pro parte. Roberty included an incredible variety of plants, representing at least half a dozen species in two genera, in this species.

Annual or perennial vines; stems slender, woody at base, primary stems numerous, mostly prostrate, radiating from thick rootstocks and forming mats, many short, lateral branches produced, the stem apices prostrate or ascending; rooting at occasional nodes with plants sometimes arising from such nodes. Indumentum of 2-armed, T-shaped trichomes; stems, leaves, inflorescence branches, and sepals glabrate to densely pubescent. Leaves shortly petiolate, the blades elliptic to subcircular, the apices obtuse to obcordate, the margins entire, slightly undulate, the bases obtuse to cuneate. Inflorescences few-flowered axillary cymes or the flowers rarely solitary, the peduncles erect; bracts small, linear or obovate. Flowers white or bluish, 5-merous; sepals unequal, quincuncially imbricate, the outer 2 mostly elliptic with obtuse apices, the middle one asymmetric, the inner 2 shorter and narrower with acute apices, all persistent in fruit; corolla tubes faintly 5-toothed, subrotate to shallowly campanulate; stamens unequal, included, the lower part of the filaments flattened, adnate to the corolla tube, glandular pubescent, and constricted around the ovary and base of the style; pollen smooth, spheroidal, 15-colpate with 5 colpi circumpolar at each pole and 5 equatorial colpi perpendicular to and alternate with the polar colpi, the tectum punctate with numerous suprategullar spinules; gynoecium of 2 united carpels, the ovary 2-locular, 4-ovulate, subglobose to cylindrical, a small disc enclosing the base, the style exceeding the stamens, the stigma lobes flattened, shortly clavate or ellipsoidal. Capsules subglobose, 4-seeded (or fewer by abortion), splitting into 2 primary and 4 or more secondary seg-

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ments. Seeds trigonous in cross section, the outer face rounded and humped, asymmetically parabolic in longitudinal section; seed coat minutely areolate and sometimes faintly ruminate, the outer 2 margins narrowly and irregularly winged.

Subtropical regions of the world with three geographically separated subspecies: subsp. *ovalifolia* in Africa, subsp. *obcordata* from Mexico and the West Indies, and subsp. *sandwicensis* in the Hawaiian Islands.

KEY TO THE SUBSPECIES OF JACQUEMONTIA OVALIFOLIA

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- - 8–15 mm long; Africa or Hawaii
 - 2. Pubescence nearly absent, occasional trichomes found on young parts, leaf blades elliptic, the apices obtuse or retuse; Africa ______ 2. subsp. ovalifolia
 - 2. Pubescence tomentose to glabrescent, leaf blades broadly elliptic to circular, the apices strongly retuse or obcordate, rarely obtuse; Hawaii ______ 3. subsp. sandwicensis

1. Jacquemontia ovalifolia subsp. ovalifolia.

Convolvulus ovalifolius Vahl, Eclog. Amer. 2: 16. 1798, non Vahl ex West, Bidrag Beskr. Ste. Croix, 271. 1793. TYPE: Guinea [now Ghana], without locality, von Rohr s.n. (c—Herb. Vahl [IDC 2201. 13: III. 4], Fig. 3; isotypes, c [IDC 2201. 13: III. 5; photo A], w). Vahl incorrectly attributed this collection to the West Indies.
C. coeruleus Schumacher, Beskr. Guineiske Pl., 101. 1827; evidently preprinted from Kongel Danske Vidensk. Selsk. Naturvindensk. Math. Afh. 3: 121. 1828, nec Sprengel in L., Syst. Veg., ed. 16. 1: 593. 1824, nec Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12: 254. 1845. TYPE: Guinea [now Ghana], without locality, Thonning 62 (c—Herb. Schumacher [IDC 2203. 25: II. 3. photo mo]; isotypes, c [IDC 2203. 25: II. 1,2]).

J. coerulea (Schumacher) Choisy ex G. Don, Gen. Syst. 4: 283. 1838.

Ipomoea oleracea Welwitsch, Ann. Conselho Ultramarino 1: 589. 1859. туре: Angola, dist. Angola, in periodically flooded dry places in the region of the sea shore, July 1858, Welwitsch, presumably LISU, not seen. Verdcourt cited Welwitsch 6252 (вм) as an isotype. I have examined three sheets of this number from вм, and none were collected in July 1858.

Stems to 3 m long, the apices usually ascending. Pubescence sparce, mostly confined to young plant parts and mature peduncles. Leaves to 9.5 cm long; petioles 0.3–3 cm long but usually 0.5–1.2 cm long; blades elliptic, the apices obtuse or retuse, the bases cuneate, to 7 cm long and 4.5 cm wide but commonly $\frac{1}{3}-\frac{2}{3}$ that size, slightly fleshy. Inflorescences 1–4.5 cm long, usually not exceeding the leaves, the lower bracts to 13 mm long and 5 mm wide but usually much smaller. Flowers bluish; outer 2 sepals elliptic or obovate, obtuse to slightly acute, 6–8 mm long and 4–6 mm wide, the middle sepal falcate, acutish, 5–6 mm long and 2–3 mm wide, the inner 2 narrowly ovate, acute, 5–6 mm long and 2 mm wide; corolla tubes 8–12 mm long; filaments 5–8 mm long, constricted around the style 1.5–3 mm from the base, the anthers 1–1.5 mm long; ovaries ovoid or cylindrical, 1–1.5 mm long, the styles 6–7 mm long, the stigma lobes 1–2 mm long. Capsules globose, 5 mm in diameter. Seeds 2.5–3 mm long. Flowering from January to August (October).

Africa south of the Sahara Desert—the Gold Coast, Portugese West Africa, and British East Africa (Fig. 9). Little is known of habitat perferences; plants

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have been collected from sandy beaches and the margins of seasonal or permanent lakes at altitudes from sea level to ca. 1000 m.

Specimens Examined

ANGOLA. Luanda: without localities, Gossweiler 165 (K); Jan 1854, Welwitsch 6252 (BM); Jul 1854, Welwitsch 6252 (BM); Aug 1858, Welwitsch 6252 (BM); without date, Welwitsch 6252 (G). Moçâmedes: Damaraland, Moçâmedes, Höpfner 21 (G); ad ripas fluminis Bero, Welwitsch 6121 (BM).

GHANA: Accra, Dalziel 8 (κ); Accra, behind beach, Irvine 668 (κ); Agric. Res. Station, Nungua, Accra Plains, Rose-Innes GC30064 (κ); without localities, Isert s.n. (c), Thonning 62 (c), von Rohr s.n. (c, w, type).

Тосо: Prope Lomé, Warnecke 254 (вм, вк, с, L).

KENYA. Baringo: Lake Baringo, *Bickford EAH11062* (κ); SW shore of Lake Baringo, in patches near shore, *Verdcourt* 3579 (BR). Kilifi: Haluabagula camp, N of Dakatcha, *Dale K1073* (κ).

SOMALI REPUBLIC: Galwin, Ciferri 105 (K).

TANZANIA. Mpwapwa: Dry floor of seasonal lake, Gombo Lake, Burtt 4630 (κ); Lake Kimagaii, Hornby & Hornby 706 (κ).

UGANDA. Bunyoro: Shore of Lake Albert, near Kibero, Bagshawe 1422 (вм, us). MADAGASCAR: Côte orientale, anno 1853, Boivin s.n. (G).

Hallier (1918) also reports this taxon from Sierra Leone (collected by Afzelius).

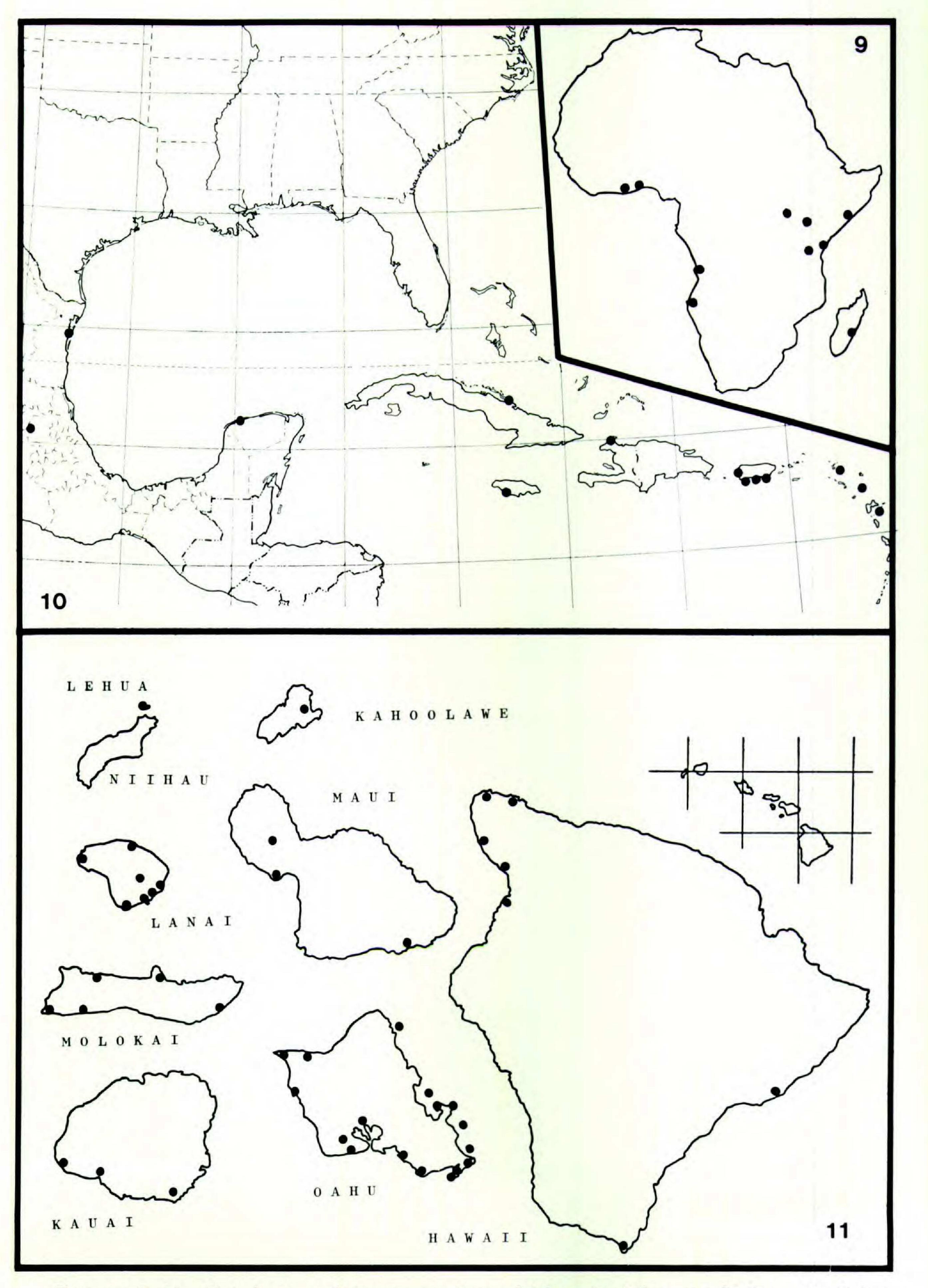
2. Jacquemontia ovalifolia subsp. obcordata (Millspaugh) Robertson, stat. et comb. nov.

Convolvulus obcordatus Millspaugh, Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 88. 1900. TYPE: Mexico, Yucatán, along the railroad about 8 km S of Progresso, 5 March 1899, Millspaugh 1707 (F, Fig. 5).

J. obcordata (Millspaugh) House, New York State Mus. Bull. 233-234: 63. 1921. J. subsalina Britton in Britton & Wilson, Sci. Survey Porto Rico & Virgin Isl. 6: 106. 1925. TYPE: Puerto Rico, Ponce, coastal marsh between Ponce and Santa Isabel, 18 March 1915, Britton & Brown 5515 (NY, photo MO; isotypes MO, NY).

Stems prostrate, to 2 m long. Pubescence sparce, mostly confined to young plant parts, petioles, and peduncles. Leaves to 5.5 cm long, usually much smaller; petioles 0.5–1.2 cm long, rarely to 2.5 cm; blades elliptic to subcircular, the apices retuse to obcordate, the bases cuneate, to 3 cm long and 2.6 cm wide, mostly $\frac{1}{4}-\frac{2}{3}$ that size, fleshy. Inflorescences 6–29 mm long, rarely exceeding the leaves; bracts linear, small. Flowers white to blue or lavender; outer 2 sepals ovate, elliptic, or broadly elliptic, obtuse to acutish, 2.5–4 mm long and 2–2.5 mm wide, the middle sepal asymmetrically ovate, obtuse to acutish, 2.5–3 mm long and 2 mm wide, the inner 2 narrowly ovate to ovate, acute, 2.5–3.5 mm long and 1.5–2 mm wide; corolla tubes 7–10 mm long; filaments 4–7 mm long, constricted around the style 2 mm from the base, the anthers 1–1.5 mm long; ovaries ovoid to globose, 1 mm long, the styles 4–5 mm long, the stigma lobes 0.75–1.25 mm long. Capsules globose, 4–5 mm in diameter. Seeds 2–2.5 mm long. Flowering from October to May, most frequently collected in February and March. Chromosome number, 2n = 18 (Jones, 1968; as J. subsalina).

Eastern Mexico, the Greater Antilles, and a few of the limestone Caribbees (Fig. 10). This subspecies is usually found in saline or alkaline soils near the coast, sometimes in marshes, around the edges of ponds, or along railroad tracks. Its occurrence is sporadic, and most populations evidently consist of only a few plants.



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FIGURES 9-11. Distribution of Jacquemontia ovalifolia.—9. Subsp. ovalifolia.—10. Subsp. obcordata.—11. Subsp. sandwicensis.

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Illustration: Britton (1930), as J. subsalina; Robertson (1971; to be published in a later paper).

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SPECIMENS EXAMINED

MEXICO. Hildago: Distr. Metztitlán. San Cristobal to main body of Laguna de Metztitlán, altitude 1200 m, Moore 2129 (сн). Tamaulipas: San José Island in Laguna Madre, LeSueur 369 (F, GH, US). Yucatán: Progresso, Millspaugh 1707 (F, type). State not known: Nueva España, Pavón s.n. (G); Sessé et al. 444 (1641) (F).

ANTIGUA. Freetown, Box 1154 (F, IJ, MICH, US); Ffryes near Bethesda, Box 1374 (MO, Us); presumably from Antigua, Wullschlägel 361 (м).

CUBA. Camagüey: Ganado, Cayo Sabinal, Shafer 865 (F, NY, US).

HAITI. Nord Ouest: Vicinity of Port de Paix, Leonard & Leonard 11739 (us), 15266 (NY, US).

JAMAICA. St. Elizabeth: Pedro Bluff, Harris 9812 (UCWI).

MARIE GALANTE. Bord de mer sur la route qui longe la mer entre Capesterre en Grand Bourg, altitude 2 m, Quentin 161 Duss 438 (A) [mixed collection?]; Questel 746 (US), 1467 (US), 1492 (US); Stehlé 1942 (US).

PUERTO RICO. Guánica: Guánica Lake, Sargent 8 (GH). Guayama: Aguirre, Britton et al. 6026 (F, NY, US); vicinity of Salinas, Britton et al. 6046 (F, NY, US). Mayaguez: Moist plain near Boquerón, Britton & Britton 9252 (NY); plain, Boquerón, Britton & Britton 9385 (GH, NY); vicinity of Boquerón, Britton et al. 8873 (NY); Boquerón Swamp, Velêz 1831 (NY); cultivated ground, Ensenada, Britton et al. 8323 (NY, US). Ponce: Between Ponce and Santa Isabel, coastal plain, Britton & Britton 5515 (F, MO, NY, US), 7339 (NY), saline plain, Britton & Britton 9451 (NY, US).

ST. BARTHÉLEMY. Grande Saline, Questel 373 (NY, US).

Subspecies obcordata has also been reported from St. John's in the Virgin Islands (Jones, 1968, as J. subsalina).

- 3. Jacquemontia ovalifolia subsp. sandwicensis (A. Gray) Robertson, stat. et comb. nov.
 - J. sandwicensis A. Gray, Proc. Amer. Acad. Arts 5: 336. 1862. LECTOTYPE: Sandwich Islands [Hawaii], Oahu, "Herbarium of the U. S. Exploring Expedition under the command of Capt. Wilkes" (US 75440, Fig. 2; isolectotypes NY, fragment GH). Gray saw all the duplicates cited; the specimen at US is selected as the lectotype because it is the best specimen and also that institution is the depository of material from the Wilkes Expedition.
 - Ipomoea ovalifolia var. pubescens Choisy, Mém. Soc. Phys. Genève 6: 449. 1834; Convolvulac. Orient., 67. LECTOTYPE: Sandwich Islands [Hawaii], Gaudichaud 26 (G); selected by Choisy in DC., Prodr. 9: 357. 1845.
 - I. ovalifolia var. tomentosa Choisy, Mém. Soc. Phys. Genève 6: 449. 1834; Convolvulac. Orient., 67. LECTOTYPE: Sandwich Islands [Hawaii], Gaudichaud 27 (G); selected by Choisy in DC., Prodr. 9: 357. 1845.
 - J. ovalifolia var. tomentosa Hillebrand, Fl. Hawaiian Isl. 318. 1888. TYPE: Hawaii, southern shore of Molokai, Hillebrand (destroyed in B).
 - Convolvulus sandwicensis (A. Gray) Bentham & Hooker ex Drake, Ill. Fl. Isl. Maris Pacifici. 245. 1892.
 - J. sandwicensis var. tomentosa fo. hosakai Degener & Degener, Fl. Hawaiiensis. Family

307. 1956. TYPE: Hawaii, Kawaihae, Waimea, Hosaka 2024 (BISH, not seen).

Stems prostrate, to 3 m long. Pubescence quite variable, stems, leaves, peduncles, and sepals with densely overlapping trichomes to merely pubescent, rarely glabrescent; some plants with all parts (except the corolla) canescent. Leaves to 6 cm long; petioles 5-15 mm long; blades elliptic to circular, the apices retuse or obcordate, the bases cuneate to attenuate, to 4.8 cm long and 3.2 cm wide, mostly $\frac{1}{3}-\frac{2}{3}$ that size, often thick and/or fleshy. Inflorescences 2-4.5 cm long, rarely reaching 9.5 cm, usually exceeding the leaves; lower bracts

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3-8 mm long, linear to obovate. Flowers pale blue to almost white; outer 2 sepals broadly ovate, broadly obovate, or broadly elliptic, 5-8 mm long and 4-6 mm wide, the middle sepal asymmetrically ovate or falcate, obtuse to acutish, 5-6 mm long and 2-5 mm wide, the inner 2 narrowly ovate, acute to acuminate, 4-6 mm long and 2-3 mm wide, the sepals enlarging with the fruit; corolla tubes 10-15 mm long; filaments 5-12 mm long, constricted around the style 2-3 mm from the base, the anthers 1-2 mm long; ovaries ovoid, 1.5 mm long; styles 7-13 mm long, the stigma lobes 1-1.25 mm long. Capsules enclosed by the accrescent sepals, quadrangular-globose, 4-6 mm in diameter. Seeds 2-3 mm long, sometimes without winged margins. Flowering all year, most frequently collected from December to July. Hawaii, all islands (except Niihau) in the major eastern group (Fig. 11). Subspecies sandwicensis is usually found near the ocean, particularly on the leeward side of the islands, in arid habitats such as dry plains, rocky slopes, and barren lava flows; the substrata are clay, coral, coral sand, and volcanic ash and cinders. According to Fosberg (1951) this taxon is one of only two strand plants of American affinities in the Hawaiian Islands (the other is Lycium carolinianum (Walter).

Illustrations: Pope (1929: 184); Degener & Degener (1956: Family 307); photograph in Carlquist (1970).

The abundance of trichomes on the leaves, inflorescence branches, and calyces varies greatly, and the full range between glabrescent and tomentose (Fig. 4) exists not only on the same island but also within the same population and even on some individual plants. Degener and Degener (1956) use the combination Jacquemontia sandwicensis var. tomentosa (Choisy) Hillebrand for plants with densely castaneous indumentum, but Hillebrand considers Ipomoea ovalifolia var. tomentosa Choisy a synonym of the glabrescent form and is clearly describing a new variety based on a different type. Plants with canescent indumentum have been called J. sandwicensis var. tomentosa fo. hosakai Degener & Degener. Because of the variability in indumentum density, I do not recognize any infrasubspecific taxa. The situation in J. ovalifolia subsp. sandwicensis seems analogous to that in Conocarpus erectus L., the buttonwood mangrove of tropical America and West Africa, in which there can be a full continuum between glabrous and densely pubescent leaves even on the same branch (Semple, 1970). Pope (1929) notes two flower colors in subsp. sandwicensis, light blue and bright blue. The native name pauohiiaka means "skirt of Hiiaka," and legend has it that the Goddess Pele bestowed this name upon the plant. Degener and Degener

relate this fable: ". . . when the Goddess returned from a protracted morning's fishing, she discovered that this plant had grown over her baby sister, Hiiaka, whom she had left on the beach, to protect her from the sun."

The leaves and other plant parts of subsp. sandwicensis have been used as a tea and in folk medicine for a variety of ailments, and the rootstocks are edible (Degener & Degener, 1956; Nagata, 1971; Pope, 1929). This plant showed positive tests with six reagents used to detect alkaloids (Swanholm *et al.*, 1959).

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SPECIMENS EXAMINED

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HAWAII. Hawaii: Between loran station and Upolu Airport, Baldwin 27296 (L); along coast, Halawa, Kohala, Degener 7143 (GH, NY); near Puako, Degener & Degener 31644 (A); coastal rocks between Mahukona and Kawaihae, Degener & Degener 31645 (A); arid barren range between Kawaihae and Waimea, Degener & Wiebke 3362 (NY, UC, US); among rocks and ash along coast, Kalae, Degener et al. 24361 (L, M, NY, US); Kaene Point, sand dunes near sea level, Webster et al. 13847 (GH); S Kohala Distr., 2 mi. SE of Kawaihae, altitude ca. 500 ft, Webster et al. 13986 (GH), 13987 (GH). Kahoolawe: E end, above Kanopou Bay, bare wind-swept ground, altitude 200-300 m, Bryan & Christophersen 731 (NY, UC); without locality, Remy 420 (GH). Kauai: In sand, Mana Airport, Alexander & Kellogg 5277 (uc, us); in littore Koloa, Faurie 1044 (G); Waimea, altitude 300 m, Hochreutiner 3622 (G). Lanai: On rocks and clay above low sea cliffs, Kalaeahole, Degener & Degener 24214 (L); arid clay, rock coast, Hulope Bay, Degener & Degener 24215 (NY, US); bare clay, arid soil, Puu Ulaula, Degener & Degener 28623 (A, M, W); red lava cinders along coast, near Manele, Degener & Degener 30110 (NY); coastal rocks, Kaunola Bay, Degener & Degener 30756 (NY, W); from grassy area to windy bare clay, Kuahua Culch, altitude 800 ft, Degener & Degener 30757 (A, NY, W); dry roadside, road 1 km N of Koele, Fosberg 12519 (A); Manele, Munro 232 (MO). Lehua: Crusty volcanic ash near lighthouse at summit of Island, Carlquist 2255 (GH, IJ, UC). Maui: Windy coast, Kaupo, Degener & Degener 27778 (L, UC); on barren hills near McGregor, Degener & Wiebke 3361 (NY, UC); arid aeolian deposits, on way to Iao Valley, Wiebke & Topping 3359 (NY, UC, US); along bank above beach near Paia, Yuncker 3451 (us); without localities, Topping 7138 (NY, US), 7144 (NY), Wawra 1923 (W), U. S. Exploring Expedition under the command of Capt. Wilkes (US, fragment GH). Molokai: Arid rocky plain near Kolo, Degener 7139 (NY); extremely arid region near sea W of Moomomi, Degener 7140 (A, NY); along coast in arid regions, Kaa, Degener 7141 (CAS, MO, NY, US); Ka Law o Ka Laau, Forbes 65 (NY); without locality, Forbes s.n. (NY); bare slopes above shore, Pohakuloa, Honoulimaloo, altitude 10 m, Fosberg 13413 (F); eroded places in dry flat volcanic soil NE of Puu Ula, Fosberg 29574 (NY); sand flat, Moomomi sand dunes, altitude 10 m, Fosberg & Fosberg 13433 (F, мо); West, open, dry ground, Hitchcock 15123 (us); West, sand dunes along coast, Hitchcock 15127 (us); Moomoni Beach, Rock 14051 (A), Rock s.n. (A, GH, US). Oahu: Kaena Point, altitude 5 m, Christophersen 1042 (NY); on sand and coral back of beach, Honouliuli, Barbers Point, Cowan 794 (uc); near coast on arid plain, Makapuu Point, Degener 2062 (uc, us); near ocean, Mokuleia Beach, Waialua, Degener & Degener 23615 (BM, NY); arid rocky clay plain overlooking the sea, Makapuu Head, Degener et al. 7142 (GH, MO, NY); along arid coast, Lahilahi [Mauna], Degener et al. 10412 (CAS, GH, KANU, L, MO, NY, US); Pearl City, Forbes 1532 (MO); Mokapu Peninsula, Pyramid Rock, Heeia Flats, Heleloa, Fosberg 10578 (us); side of gully near ocean, Ulupau Head, Mokapu Peninsula, altitude 2 m, Fosberg 10902 (F); eroded slope, Mokulua, S islet, Kaiua, altitude 15 m, Fosberg 12889 (A, F, UC, US); thin coral sand on basalt, Kaohikaipu Island, Waimanalo Bay, altitude 3 m, Fosberg 14057 (F); sandy coral soil on raised reef, Kapapa Island, Keneohe Bay, altitude 2 m, Fosberg & Egler 14012 (F, US); calcareous sandstone, Mokuauia Island, Laie Bay, altitude 4 m, Fosberg & Egler 14162 (A, CAS, F, US); Diamond Head, Heller 2095 (BM, F, GH, MO, NY, UC, US, W); Macrae, Herb. Hillebrand 395 (GH); Honolulu, Fort Shafter, Hitchcock 13851 (Us); coral plain near beach, Ewa, Barbers Point, Hosaka 1353 (F, W); top of bluffs above Hanauma Bay, altitude 50-100 ft, Hutchinson & Obata 2846 (F, NY, UC, US); without locality, Mann & Brigham 619 (F, G, GH, MO, NY, US); Honolulu, Meebold 8373 (м); Koko Head, Meebold 24963 (м); Koko Head region, 6 Aug 1930, Neal s.n. (UC); Waimanalo, Pickering & Seamster 3358 (F); Waialua, anno 1911, Rock s.n. (GH); Mokuleia Beach Park, foremost sandy dunes, von Royen 10198 (A); Koko Head, wind-swept volcanic stone slope near sea, van Steenis 20401 (L); Koko Head Crater, Topping 3032 (NY); beside road up Mokapuu Head, Wilbur 502 (US); without locality, Herb. U. S. Exploring under the command of Capt. Wilkes (us, fragment GH, type). Island Unknown: Chamisso 163 (F); Gaudichaud 26 (G), 27 (G), 245 (G); Hillebrand s.n. (US, W).

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